

B R E V I O R A

Museum of Comparative Zoology



US ISSN 0006-9698

CAMBRIDGE, MASS.

9 MAY 2018

NUMBER 560

HERPETOFAUNA OF CAY SAL BANK, BAHAMAS AND PHYLOGENETIC RELATIONSHIPS OF *ANOLIS FAIRCHILD*, *ANOLIS SAGREI*, AND *TROPIDOPHIS CURTUS* FROM THE REGION

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ABSTRACT. Although the terrestrial herpetofauna of the Bahamas Archipelago is largely well characterized, many smaller or outlying islands and island banks are poorly studied owing to their remoteness. The Cay Sal Bank is an uninhabited island bank lying between the Florida Keys and western Cuba. Politically a part of the Commonwealth of the Bahamas, the Cay Sal islands are disjunct from the rest of the Bahamas Archipelago to the east. The bank supports 117 small emergent islands around its perimeter, on which at least six species of squamates have been recorded. Recent expeditions have added to this species list, although several islands remain unsurveyed. Of these six squamate species, only *Anolis fairchildi* is considered endemic to the bank. The evolutionary relationships of the other species are speculated to derive from either Bahamian or Cuban progenitors. Here we report on a recent expedition to the Cay Sal Bank, and provide updated and novel island records. We further characterize the two native *Anolis* species and one *Tropidophis* species using molecular phylogenetic analyses to estimate the likely origins and divergence times of these species. We find that both *Anolis* species are recently (< 2 Mya) derived from, and likely conspecific with, west Cuban ancestors, whereas the *Tropidophis* is likely conspecific with the populations of *Tropidophis curtus* on the Great Bahamas Bank. Thus the terrestrial squamate herpetofauna on the bank are a product of dispersal from both the Great Bahamas Bank to the east and western Cuba to the south. We provide an updated understanding of the biogeography and evolutionary history of these squamates on the Cay Sal Bank.

KEY WORDS: Bahamas; mitochondrial DNA; phylogenetics; systematics

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INTRODUCTION

The terrestrial herpetofauna of the Bahamas Archipelago has been well studied over the last century (e.g., Barbour, 1906; Cochran, 1934; Barbour and Shreve, 1935; Knapp et al., 2011). A series of compendia has collated island herpetofaunal records into comprehensive resources (MacLean et al., 1977; Schwartz and Henderson, 1991; Henderson and Powell, 2009; Buckner et al., 2012), demonstrating the breadth and depth of our understanding of herpetofaunal diversity and distribution in the archipelago. Nevertheless, some portions of the region remain understudied, largely owing to difficulty accessing remote islands. Recent studies of remote islands, such as the Great Isaac Cays, Ragged Islands, and the Conception Bank, has led to the further characterization of island herpetofaunal distributions (Winchell et al., 2015; Geneva et al., 2016; Reynolds et al., 2016a; Reynolds and Puente-Rolón, 2016a) and the discovery of new species (Reynolds et al., 2016b).

The Bahamas Islands are a political unit, administered by the Commonwealth of The Bahamas, which encompasses a series of island banks occupying a triangle between the Greater Antilles, peninsular Florida (U.S.A.), and the North Atlantic Ocean. This region, when inclusive of the geologically cohesive (yet politically separate) Turks and Caicos Archipelago, is referred to as the Lucayan Archipelago and stretches $> 1,360$ km from northwest to southeast ($19^{\circ}84' - 27^{\circ}30'N$, $68^{\circ}70' - 80^{\circ}54'W$). This archipelago is composed of a complex of large and small carbonate platforms (banks) supporting hundreds of emergent islands. These island banks are generally inundated by water no greater than 20–40 m deep, whereas depths of water between banks can reach thousands of meters (Purkis et al. 2014). During intra-glacial periods a much greater portion of

these banks was emergent, resulting in substantially larger landmasses than are currently present, although the deep channels separating banks have maintained their isolation from one another and from Florida and the Greater Antilles. The terrestrial herpetofauna of the Lucayan Archipelago is composed of lineages derived from over-water colonization from Hispaniola and Cuba, with some endemism having likely evolved in situ (Hower and Hedges, 2003; Hedges and Conn, 2012; Knapp et al., 2011; Reynolds et al., 2013, Geneva et al., 2015; Reynolds et al., 2016b).

To the west of the Lucayan Archipelago lies the Cay Sal Bank, an isolated and uninhabited carbonate platform administered by the Commonwealth of The Bahamas. This relatively small ($4,000 \text{ km}^2$; Goldberg, 1983) bank lies between peninsular Florida, Cuba, and the Great Bahamas Bank, and is bounded by the Florida Straits to the north, the Santaren Channel to the east, and the Nicholas Channel to the south (Fig. 1). Previously an exposed landmass 11,000 years ago, the Cay Sal Bank was largely inundated over the subsequent 5,000 years owing to sea-level rise and slight bank subsidence (Purkis et al., 2014). Presently water depths range from 0.5 to 20 m across facies of the bank (Goldberg 1983; Bruckner et al. 2014; Purkis et al., 2014). The edges of the bank are bounded by deep drop-offs, with water depths declining rapidly from 30 to 1000 m. Portions of the bank edges support a maximum of 117 low-lying islands (< 10 m above sea level), most of them with little vegetation, representing a total land area of 484 ha (Mackin et al., 2015). Most of these islands are small rocks less than 20 ha in area, whereas six larger islands range from 29 to 150 ha in area (Goldberg, 1983; Krysko et al., 2015).

The islands of the Cay Sal Bank were first described from a zoological perspective by

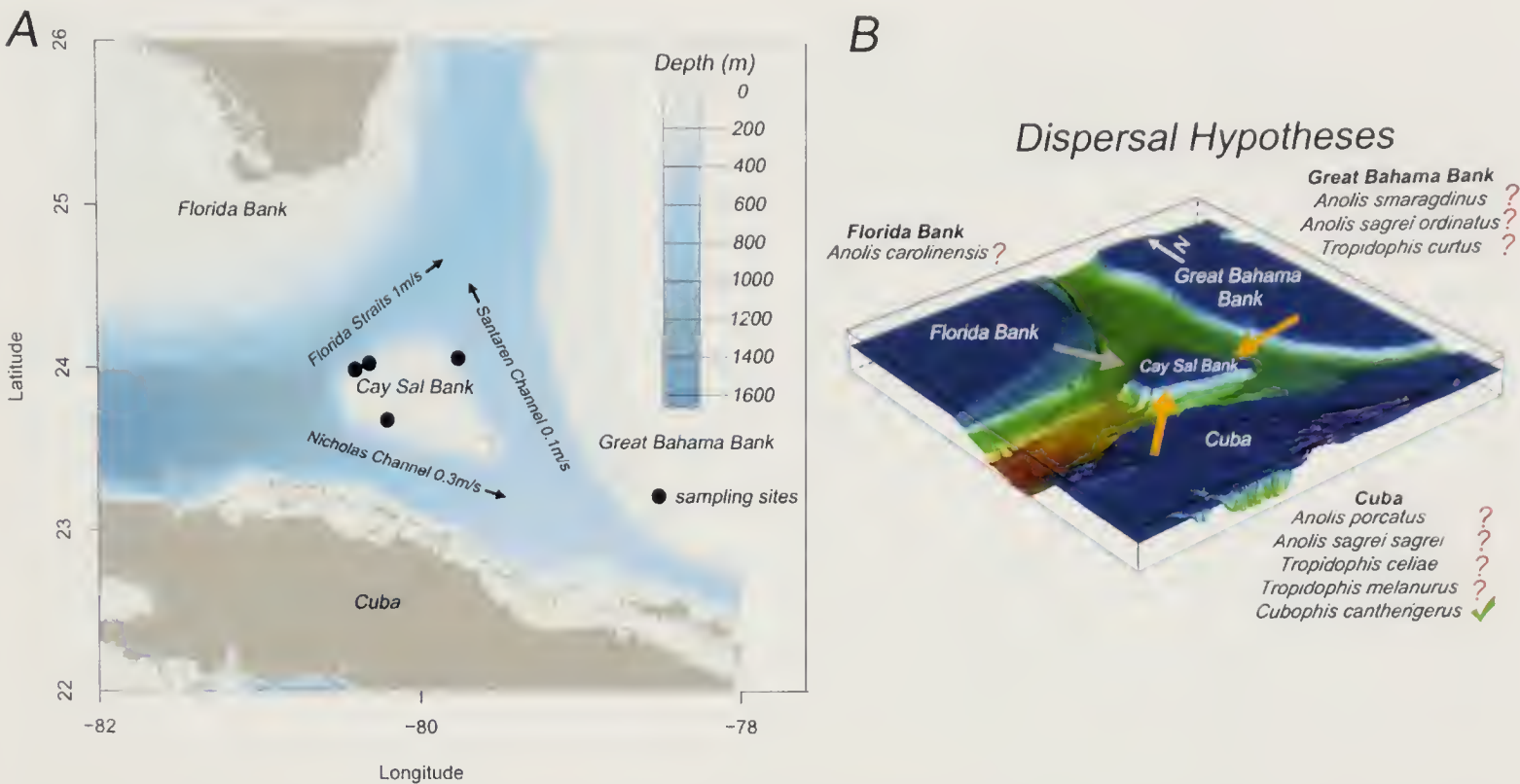


Figure 1. A, map of study region, including the Cay Sal Bank and the surrounding Florida, Cuba, and Great Bahama banks. Water depth information is indicated by blue colors, and the three currents surrounding the Cay Sal Bank are shown with approximate flow rates (from Purkis et al., 2014). Note that Goldberg (1983) incorrectly represents the direction of flow of the Nicholas Channel. Sampling sites on the Cay Sal Bank are shown as red circles. B, dispersal hypotheses for terrestrial squamate reptiles serving as potential progenitors of Cay Sal Bank species. The study region is shown as a three-dimensional map with bathymetric data on the z-axis. Potential progenitor species are shown adjacent to their respective banks, with green check marks indicating confirmed dispersal and red question marks indicating possible dispersal. Orange arrows indicate likely dispersal trajectories to the Cay Sal Bank from either Cuba or the Great Bahama Bank, the latter of which is currently considered to be the likely pathway for squamate colonization. The gray arrow indicates that dispersal of green anoles (*Anolis carolinensis*) from Florida is possible, although unlikely, owing to the strength of the current in the Florida Straits.

Agassiz (1894) during a cruise through the region. Since that time some notable expeditions to the region have increased our knowledge of the biodiversity of the bank (Cory, 1891; Buden and Schwartz, 1968; Goldberg, 1983; Purkis et al., 2014; Krysko et al., 2015; Mackin et al., 2015). Six extant species of squamate reptiles occur on the Cay Sal Bank, and are thought to be derived largely from the Bahamas to the east, as most are considered conspecific with Bahamian subspecies (Table 1; Buden and Schwartz, 1968; Buckner et al., 2012). The squamate diversity of the Cay Sal Bank was first described by P. Bartsch between 1928 and 1930 (in Cochran, 1934), who identified two *Anolis* lizards (*A. sagrei* and *A. fair-*

childi) and one *Tropidophis* snake (*T. curtus*; Cochran, 1934; Buden and Schwartz, 1968). Thomas later found the gekkonid lizard *Sphaerodactylus nigropunctatus* and the scolecophidian blindsnake *Typhlops biminensis* in 1967 on Elbow Cay (Buden and Schwartz, 1968; Thomas, 1968a). Recently the Cuban colubrid snake species *Cubophis cantherigerus* was discovered on the Anguilla Cays at the southeastern edge of the Bank (Krysko et al., 2015), suggesting that additional exploration of the region might continue to resolve species diversity, distribution, evolutionary relationships, and biogeographic origins of the terrestrial herpetofauna. Of these six squamate species, *A. fairchildi* is the only presently recognized endemic reptile

TABLE 1. ISLANDS ON THE CAY SAL BANK WITH KNOWN AND NEWLY DOCUMENTED TERRESTRIAL HERPETOFAUNAL RECORDS. NO RECORD INDICATES THAT NO HISTORICAL RECORD EXISTS FOR THAT ISLAND, AND THAT NO SPECIMENS WERE OBSERVED ON THAT ISLAND DURING OUR RESEARCH CRUISE. RECORDS ARE FROM BUCKNER ET AL. (2012), WHICH IS A COLLECTION OF PREVIOUSLY DOCUMENTED RECORDS FROM A VARIETY OF SOURCES. ASTERISK INDICATES ISLANDS THAT WERE VISITED ON OUR RESEARCH CRUISE. NEW ISLAND RECORDS ARE IN BOLD TEXT.

Island	Coordinates	~ Area (km ²)	<i>Anolis</i> <i>sagrei sagrei</i>	<i>Anolis</i> <i>fairchildi</i>	<i>Tropidophis</i> <i>curtus</i>	<i>Cubophis</i> <i>cantherigerus</i>	<i>Sphaerodactylus</i> <i>unigropunctatus</i> <i>flavicauda</i>	<i>Typhlops</i> <i>bininiensis</i> <i>bininiensis</i>
Cay Sal*	23°41'24"N, 80°23'24"W	1.22	documented, observed	documented, observed	no record	no record	no record	no record
Elbow Cay*	23°57'36"N, 80°26'23.9994"W	0.32	documented, observed	no record	documented, observed	no record	documented, not observed	documented, not observed
East Double Headed Shot Cay*	23°59'23.9994"N, 80°20'24"W†	0.20	new record	no record	documented, not observed	no record	no record	no record
Great Dog Rock*	24°1'48"N, 79°49'47.9994"W	< 1.0	new record	no record	no record	no record	no record	no record
Elephant Rocks*	23°55'47.9994"N, 80°28'11.9994"W	?	new record	no record	no record	no record	no record	no record
Cotton Cay (Anguilla Cays)	23°29'23.9994"N, 79°30'36"W	1.45	documented	documented	no record	no record	no record	no record
Anguilla Cays	23°34'12"N, 79°35'24"W	0.62	documented	no record	no record	documented	no record	no record
Damas Cays	23°52'12"N, 79°46'11.9994"W	?	no record	no record	no record	no record	no record	no record

†Note that this is given incorrectly as 23°55'47.9994"N, 80°28'11.9994"W in Buckner et al. (2012).

found on the Cay Sal Bank, and is thought to be derived from Cuban ancestors (Glor et al., 2005).

Here we define herpetofauna to include the terrestrial reptilian and amphibian fauna (the latter of which lacks representation on the Cay Sal Bank), and thus excludes marine turtles. We provide a comprehensive review of herpetofaunal records from the Cay Sal Bank on the basis of published accounts and the results of an expedition we conducted to the region in August 2015. We also provide island accounts, including descriptions of terrestrial habitats and herpetofaunal records for each major island on the bank. We infer the phylogenetic relationships of three terrestrial species and their close congeners, which, when combined with other known information on the historical biogeography of other species, provides a clear picture for the origins of this depauperate and isolated herpetofaunal community.

MATERIALS AND METHODS

Research cruise

We (RGR and ARPR) traveled to the Cay Sal Bank aboard a chartered vessel, spending 4 days and 3 nights (11–14 August 2015) on the Bank (Reynolds and Puente-Rolón, 2016b). During this cruise, our ability to sample islands was limited by weather and safety considerations; nevertheless, we were able to diurnally survey five islands across the Bank (Figs. 1, 2). Elephant Rocks and Double Headed Shot Cay are technically comprised of two islands each, separated by narrow channels, although we treat them here as single units. Surveys involved spending between 1 and 8 hours on each island, depending on the island size, during which time we sampled all available habitats using visual encounter surveys and turning over cover objects.

Genetic data and analyses

We collected three tissue samples of *A. fairchildi* from Cay Sal Island, Bahamas (23°41'26.8476"N, 80°23'23.9964"W), the only island on which we observed them. We collected tissue samples of *A. sagrei* from five islands across the Cay Sal Bank: Great Dog Rock ($n = 3$; 24°1'57.0354"N, 79°50'0.9168"W), Cay Sal ($n = 29$; 23°41'26.8476"N, 80°23'24.3564"W), Elbow Cay ($n = 11$; 23°57'17.0028"N, 80°26'32.64"W), Double Headed Shot Cay ($n = 2$; 23°59'32.82"N, 80°20'14.2794"W), and Elephant Rock ($n = 10$; 23°55'44.9796"N, 80°28'10.5312"W). Finally, we collected one tissue sample from *Tropidophis curtus* on Elbow Cay (23°57'23.3886"N, 80°26'25.6014"W), Cay Sal Bank.

We extracted whole genomic deoxyribonucleic acid (DNA) from tissue samples of the three terrestrial squamate species using the Wizard SV® kit (Promega, Madison, Wisconsin) and subsequently stored extracts at –20°C. We used polymerase chain reaction to amplify fragments of the mitochondrial genome for *Anolis* tissue samples (nicotinamide adenine dinucleotide subunit 2 [ND2]; primers from Macey et al., 1997; conditions in Revell et al., 2007) and *Tropidophis* tissue samples (cytochrome *b* [CYTB]; primers and conditions in Reynolds et al., 2013). Cytochrome *b* has been shown to be useful in species identification in boas (Campbell, 1997; Burbrink, 2004; Reynolds et al., 2013); nevertheless, we additionally sequenced three protein-coding nuclear loci for our *Tropidophis* sample (primers and conditions in Reynolds et al., 2013, 2014): neutrophin-3 (*ntf3*), brain-derived neurotrophic factor (*bdnf*), and bone morphogenetic protein 2 (*bmp2*). We purified and sequenced products in both directions on an automated sequencer (ABI 3730XL) at the Massachu-

setts General Hospital DNA Core facility, Cambridge, Massachusetts and the Genomic Sciences Laboratory at North Carolina State University, Raleigh, North Carolina. We assembled contigs and manually verified ambiguous base calls using Geneious® 10.2.1 (Biomatters, Auckland, New Zealand). We resolved heterozygous nuclear sequences using PHASE v. 2.1 (Stephens et al., 2001; Stephens and Donnelly, 2003) implemented in DnaSP v5.10.1 (Librado and Rozas, 2009) using default parameters for 100 iterations with a burn-in of 100, and a cutoff of posterior probabilities (PP) > 0.7 for base calling.

To determine the phylogenetic relationship of *A. fairchildi* relative to other Cuban and Bahamian green anoles, we mined additional ND2 sequences representing *A. carolinensis* clade green anoles (*sensu* Nicholson et al., 2012) from Genbank (data largely from Glor et al., 2004, 2005; Kolbe et al., 2007). We additionally obtained tissues from the Bahamian green anole species *A. smaragdinus* from South Bimini ($n = 2$) and Great Ragged ($n = 2$) islands, representing the northern and southern edges of the western Great Bahamas Bank (Fig. 1) in separate expeditions. These samples were extracted and sequenced as above.

To ascertain the origins of Cay Sal Bank *A. sagrei*, we subsampled (from our collected tissue samples) representatives from four of the five islands (Cay Sal, Elbow Cay, Elephant Rocks, and Great Dog Rock). We then aligned our ND2 sequences as above with a data set containing 295 haplotypes of *A. sagrei* sampled from the entire range of the species. This includes individuals from across the Bahamas and Cuba, as well as additional Caribbean lineages.

To identify phylogenetic affinities of the *Tropidophis* sample we obtained from Elbow

Cay, Cal Sal Bank, we aligned our mitochondrial CYTB and nuclear *ntf3*, *bdnf*, and *bmp2* sequences with others from GenBank or generated de novo, focusing on species with likely relationships to Cay Sal Bank animals. We included novel sequences from representative samples ($n = 2$) of *T. curtus* from Long Island, Bahamas (Table 1). We also added all available nuclear and mitochondrial sequence data for *Tropidophis*, the ingroup *Trachyboa*, and the outgroup *Tropidophis taczanowski* (see Reynolds et al., 2014) obtained from GenBank and from the alignments in Reynolds et al. (2014).

For all three data sets, and for each locus separately, we aligned our novel and GenBank sequences using the ClustalW 2.1 (Larkin et al., 2007) algorithm implemented in Geneious using reference sequences and default parameters. For the *Tropidophis* data set, we additionally created a concatenated alignment of both mitochondrial DNA and nuclear DNA sequences. Alignments are publicly available on GitHub (<https://github.com/caribbeanboas/>).

We selected the best-fit model of molecular evolution for the ND2 locus (TrN + I + G) and CYTB locus (HKY + I + G) using the Bayesian information criterion in jModel-Test2 (Guindon and Gascuel, 2003; Darriba et al., 2012). We conducted separate maximum-likelihood (ML) analysis for each alignment (green anoles, brown anoles, and concatenated *Tropidophis*) using the RAxML algorithm (Stamatakis, 2006) implemented in the RAxML plug-in for Geneious. We used the GTRGAMMA model and the rapid bootstrapping algorithm with 1,000 bootstrap (BS) replicates followed by the thorough ML search option with 100 independent searches. We consider BS values above 70% to indicate relatively well-supported clades (Felsenstein, 2004).

To estimate divergence times across the *Anolis* mitochondrial gene trees, we inferred

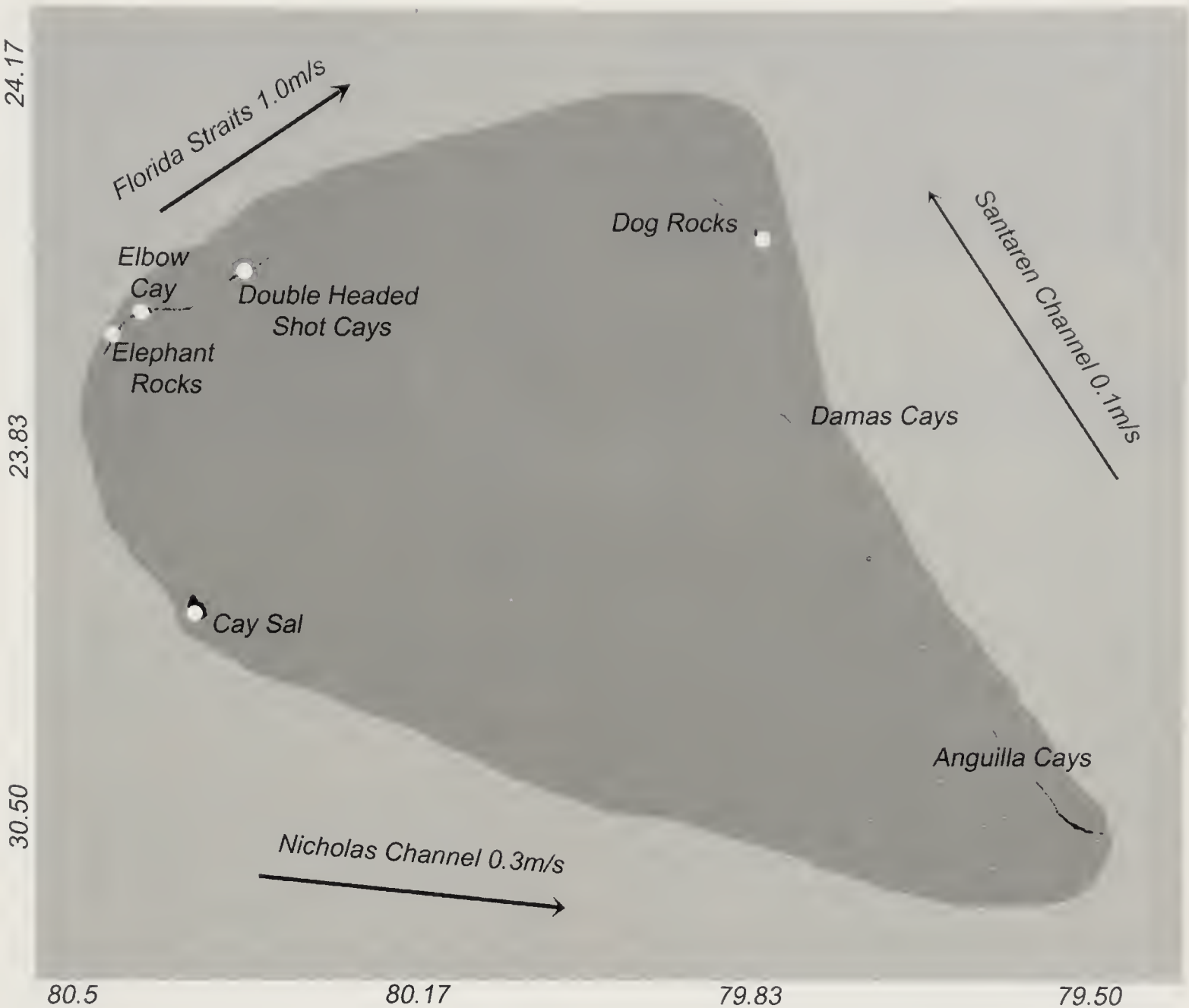


Figure 2. Major islands on the Cay Sal Bank, with currents and current speeds indicated on the bank edges. White circles indicate islands visited during our cruise.

time-calibrated Bayesian ND2 coalescent trees in the program Beast v1.8 (Drummond et al., 2012) using a relaxed molecular clock model and a rate of molecular evolution of 0.65% divergence per lineage, per million years. This rate has been previously used for the ND2 locus in other lizards (Macey et al., 1998), including many studies of Caribbean anoles (e.g., Gartner et al., 2013; Geneva et al., 2015). We furthermore note that we are primarily interested in the relative rather than absolute divergence times, and thus our analyses will be largely insensitive to the specific molecular clock rate used. We ran a

separate BEAST analysis for the concatenated *Tropidophis multilocus* data set. For each of the three separate BEAST analyses, we ran the Markov chain Monte Carlo for 100 million generations using the TrN + I + G substitution model, a Yule speciation prior, and an uncorrelated lognormal relaxed molecular clock model. We repeated each analysis three times with different starting numbers, sampling every 10^4 generations and discarding the first 25% of generations as burn-in. We assured adequate mixing of the chains by calculating the effective sample size values for each model

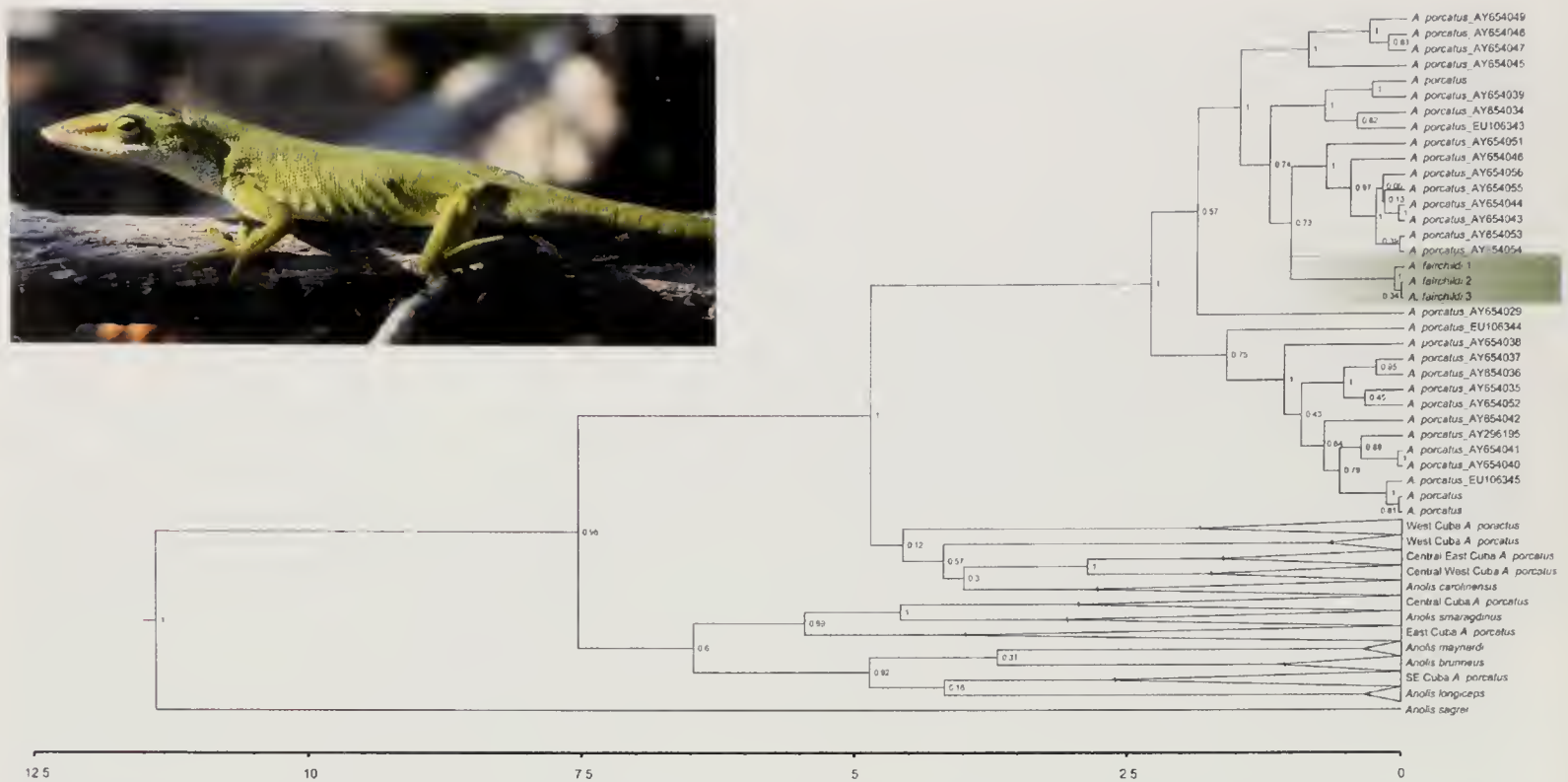


Figure 3. Bayesian phylogeny of Cuban green anole species (*carolinensis* clade), with major Cuban clades, other recognized species, and outgroups collapsed at the bottom. The clade containing *Anolis fairchildi* samples from Cay Sal Island is expanded, with *A. fairchildi* in green, consisting of an *A. porcatius* lineage from western Cuba. Numbers at nodes are posterior probabilities. The scale bar at the bottom represents coalescent times in Mya. *Anolis fairchildi* from Cay Sal Island is shown top left (photo by RGR).

parameter, with values > 200 indicating adequate sampling of the posterior distribution. We assessed convergence of the independent runs by a comparison of likelihood scores and model parameter estimates in Tracer v1.5 (Rambaut et al., 2013). We combined the results from the three analyses using Logcombiner and generated a maximum clade credibility tree using TreeAnnotator.

RESULTS

Our surveys of five islands across the Cay Sal Bank resulted in some updated distributions of the terrestrial herpetofauna (Table 1). We found *A. sagrei* on additional islands, and failed to find evidence of *A. fairchildi* outside of Cay Sal Island despite additional records in Buckner et al. (2012). Additional details are provided in the species accounts below.

For the *A. fairchildi* mitochondrial data set, we obtained a 1,172 base-pair (bp) alignment for 224 haplotypes of the eight recognized *A. carolinensis* clade species, including representative Cuban species (*A. porcatius*, *A. allisoni*) from across Cuba, and Bahamian species (*A. smaragdinus*, *A. brunneus*) from across the Bahamas. Our three *A. fairchildi* samples are nearly identical to each other and reciprocally monophyletic with respect to other *carolinensis*-clade lineages (Fig. 3). We found that *A. fairchildi* is likely a branch of the West Cuban *A. porcatius* lineage, with an estimated coalescent time of 1.05 Mya (BS = 37; PP = 0.73; 95% highest posterior density [HPD] = 0.6–1.6 Mya; Fig. 3), and thus is not closely related to Bahamian *A. smaragdinus*.

We aligned 1,092 bp of mitochondrial DNA from Cay Sal *A. sagrei* with 296 sequences of *A. sagrei* from across the range of the species. We found phylogeographically concordant sequences on the Cay Sal



Figure 4. Bayesian phylogeny of the Cuban brown anole, *Anolis sagrei*, complex, with major Cuban clades, sister species, and outgroups collapsed. Blue represents the *A. sagrei* individuals sampled from islands on Cal Say Bank, and numbers at nodes are posterior probability values. The scale bar at the bottom represents coalescent times in Mya. *Anolis sagrei* from Cay Sal Island is shown top left (photo by ARPR).

Bank, with generally well-supported reciprocally monophyletic groupings from Cay Sal Island, Elbow Cay, Elephant Rocks, and Dog Rocks (Fig. 4). We also found evidence for east–west divergence across the Cay Sal Bank, with the previously unreported Dog Rocks population exhibiting a minimum of 0.35% mitochondrial DNA divergence from the west Cay Sal Bank populations (Elbow Cay). Further, we find that Cay Sal Bank *A. sagrei* are not sister to Bahamian *A. sagrei*, as previously suggested (e.g., Buden and Schwartz, 1968; Buekner et al., 2012), but are instead sister to west Cuban *A. sagrei* lineages (Fig 4). Cay Sal populations share a mean coalescence time of 2.16 Mya with these geographically proximate Cuban populations (BS = 43; PP = 0.73; 95% HPD = 1.71–2.66 Mya).

Our Cay Sal Bank *Tropidophis* specimen exhibited a light rosy coloration (Fig. 5), which has not been reported from other populations of *T. curtus* in the Bahamas, although the dorsal patterning is similar (Fig. 6; Schwartz and Henderson, 1991; Tolson and Henderson, 1993). Additional morphological description of the specimen follows below. We aligned 3,976 bp of mitochondrial and nuclear sequence data generated from this specimen with 14 other taxa obtained from Genbank, including three from Bahamian *T. curtus*, one from Caymanian *T. schwartzi*, one Cuban *T. feicki*, and six Hispaniolan-derived *T. greenwayi* and *T. haetiannus*. We find that Cay Sal *Tropidophis* is likely conspecific with *T. curtus*, as it is minimally divergent (0.6%) from Bahamian sequences obtained from the eastern end of the Great Bahamas Bank

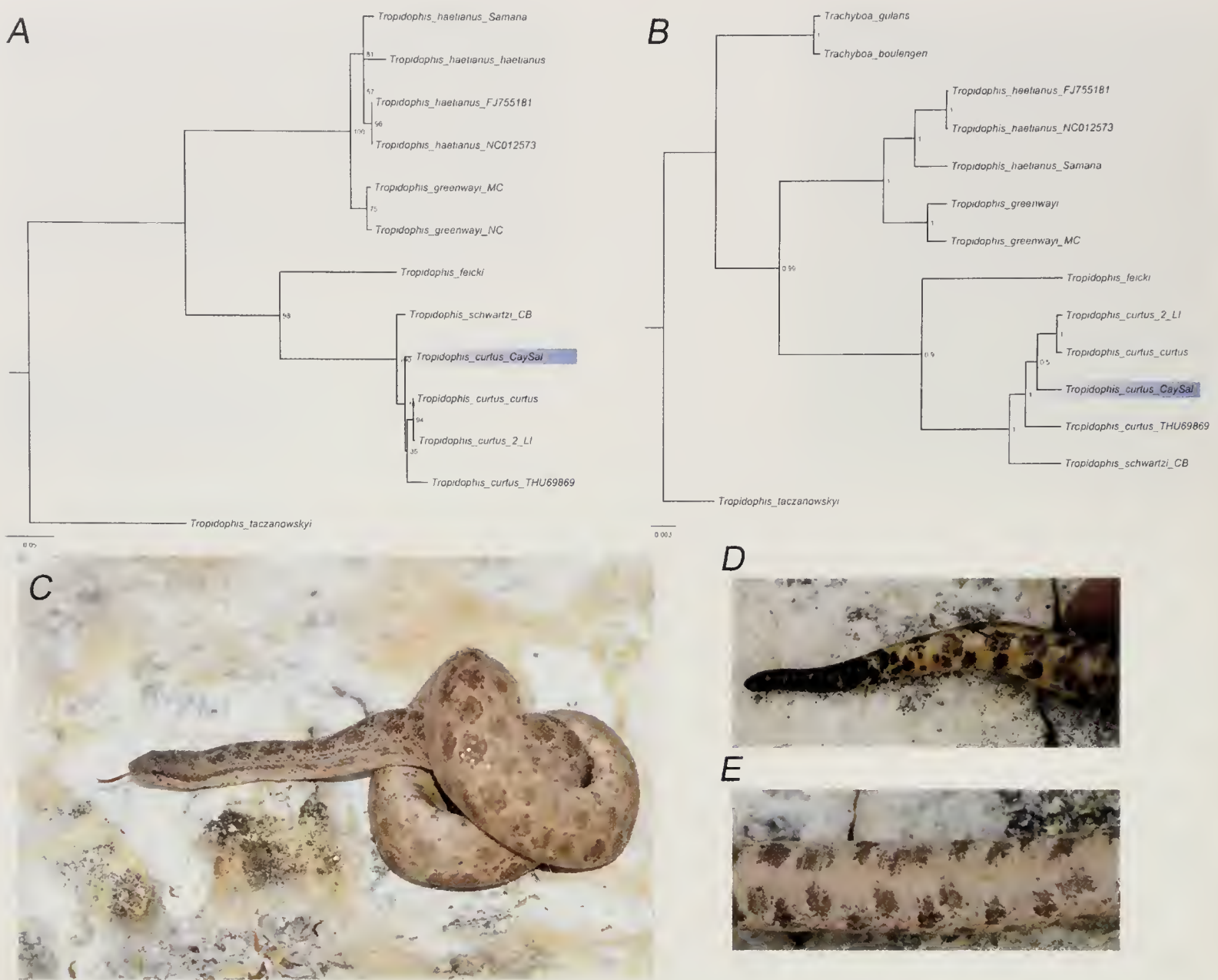


Figure 5. Phylogenetic trees for our *Tropidophis* data sets (top) and photos of the specimen of *Tropidophis curtus* encountered on Elbow Cay, Cay Sal Bank. A, maximum-likelihood tree depicting relationships among 1,083 base pairs of mitochondrial cytochrome *b* sequence data, including Cay Sal *T. curtus* (in blue). Nodes indicate bootstrap support. B, Bayesian phylogenetic reconstruction of concatenated mitochondrial DNA and three nuclear genes for *Tropidophis*, with Cay Sal *T. curtus* in blue. Nodes represent posterior probabilities. C, photo of *T. curtus* from Cay Sal Bank; D, photo of tail; E, photo of venter. Photos by ARPR and RGR.

(Long Island). Indeed, we find weak support (BS = 74; PP = 0.50) for distinctiveness of this specimen from *T. curtus* in concatenated ML and Bayesian analyses (Fig. 5).

DISCUSSION

Species accounts

Anolis fairchildi. *Anolis* lizards in the West Indies are one of the best-studied examples of an adaptive radiation—the remarkable

evolution of various forms from a single ancestral lineage. Speciation and diversification in the region have led to the present recognition of hundreds of anoline species. Green anoles, specialized to occupying the upper trunks and canopies of trees, have evolved independently on many of these islands, including Cuba. The Cuban green anoles have since colonized other regions, including the Bahamas, the southeastern United States, the Cayman Islands, and coastal Central America (Williams 1969;



Figure 6. Two *Tropidophis curtus* individuals from Long Island, Bahamas, on the Great Bahama Bank about 520 km to the southeast of Elbow Cay, showing brown and gray morphs present in those populations. Photos by RGR.

Schwartz and Henderson, 1991). This diaspora has diversified such that several these populations are recognized as different species. Within this group, eight species are recognized, and evolutionary relationships are known for all but *A. fairchildi* (Glor et al., 2005). Morphological features, such as the relatively large size of *A. fairchildi* (Barbour and Shreve, 1935; Buden and Schwartz, 1968; this work), suggested that it might have evolved from a historical colonization from Cuba. An alternative is that this species colonized Cay Sal from the Bahamas (Cochran, 1934; Buden and Schwartz, 1968), or from the North American mainland. Determining if *A. fairchildi* is more closely related to green anoles from Cuba, the Bahamas, or elsewhere using morphological data is complicated by patterns of morphological convergence in West Indian anoles that can cloud evolutionary relationships (Glor et al., 2005), and this is clear among *carolinensis*-clade *Anolis* (Buden and Schwartz, 1968). Barbour and Shreve (1935) in their description of the species suggested that *A. fairchildi* is morphologically similar to *A. smaragdinus* and *A.*

porcatus, but that it differs from the two owing to *A. fairchildi*'s larger dorsal and temporal scales. Oliver (1948) suggested that Bahamian *Anolis* and *A. porcatus* were conspecific with *A. carolinensis*. These authors (Barbour and Shreve, 1935; Buden and Schwartz, 1968) also indicated differences in coloration, particularly dorsal white spotting in *A. fairchildi*, although it should be noted that they were working with preserved specimens. Buden and Schwartz (1968) examined meristics and squamation of *A. fairchildi* in relation to other *carolinensis*-clade anoles, determining that head squamation allows diagnosis of this species. Our samples came from three male *A. fairchildi* of relatively large size (70, 73, and 74 mm snout-vent length). Their dewlaps were relatively small, with a pinkish hue and interspersed white scales. Nevertheless, given the characteristics offered by Barbour and Shreve (1935), Oliver (1948), and Buden and Schwartz (1968), morphological diagnosis of this species without knowing a specimen's provenance would be extremely challenging, with maximum male body size the only character suggesting a relationship to *A.*

porcatus (Buden and Schwartz, 1968). We observed minimal light dorsal spotting in *A. fairchildi* on Cay Sal, with this coloration owing to white and light blue scales occasionally clustering in groups of two.

Before the present study, it was unclear how long this species had been on Cay Sal, or even whether these anoles diverged sufficiently to be considered a valid species (under the phylogenetic species concept). Our molecular phylogenetic results can overcome some of the limitations of a strictly morphological data set, and also provide insight into the magnitude and timing of divergence of this species from its closest relatives. Here we are able to determine that *A. fairchildi* colonized Cay Sal from Cuba, and not from the Bahamas or Florida (hypotheses in Fig. 1B); coalescent times indicated that this colonization occurred within the late Pleistocene; and although this species might be considered conspecific with *A. porcatus* (to avoid paraphyly of the latter species), its unique geographical isolation and (possibly) diagnostic morphological features might lead to continued recognition as a unique lineage. More generally, a revision of this group might be needed—populations currently recognized as *A. porcatus* are far more divergent from each other than some are from not only *A. fairchildi* but also from *A. allisoni*, *A. brunneus*, *A. carolinensis*, *A. longiceps*, *A. maynardi*, and *A. smaragdinus* (Glor et al., 2005). We refrain from performing any revision here because our sampling of genetic loci and green anole populations was intended to only provide insights into the evolutionary relationships of *A. fairchildi* and is insufficient for a full treatment of the group.

Anolis sagrei. *Anolis sagrei* is a widely distributed species and is thought to have the largest natural range of any West Indian *Anolis* lizard (Williams, 1969). Populations on the Cay Sal Bank are described as

representatives of the Bahamian subspecies *A. s. ordinatus*, implying a natural dispersal westward or northward across the Santaren Channel. Bahamian populations of *A. sagrei* were recognized as a separate subspecies, *A. s. ordinatus*, owing to presumed differences in dewlap color and contacting supraorbital scales (Barbour, 1937; Oliver, 1948). Cay Sal specimens were assigned to *A. s. ordinatus* on the basis of similar body sizes and some head squamation similarities (Buden and Schwartz, 1968).

Contrary to these expectations, we found that the five Cay Sal Bank populations we sampled are derived from Cuban progenitors. Because our alignment included fine-scale sampling across the native range of *A. sagrei*, we infer a west-Cuban origin of Cay Sal populations, likely near Havana, Pinar de Río, or Matanzas provinces. Further, Cay Sal populations from across the bank are monophyletic with respect to their Cuban ancestors, suggesting a single colonization event, or at least the persistence of a single lineage (owing to lineage sorting). The widespread range of *A. sagrei* appears to be the result of many independent dispersal events from Cuba to elsewhere in the West Indies (Kolbe et al., 2004). Our time-calibrated phylogeny suggests that *A. sagrei* colonized Cay Sal around the time when the species also dispersed to the Swan Islands and Mesoamerica, but more recently than out-of-Cuba dispersals to the Lucayan Archipelago and the Cayman Islands (Cayman Brac and Little Cayman).

Tropidophis curtus. *Tropidophis curtus* is recorded from the Cay Sal Bank and from across the Great Bahamas Bank (Buckner et al., 2012). Before this study, only three records existed from the Cay Sal Bank, consisting of two specimens from Elbow Cay (KU KUH 269003–04; R. Thomas 1967) and one juvenile female specimen from Double Headed Shot Cay (USNM Amphib-

ians & Reptiles 81536; listed as “anon. 1930” in accessioned record at the National Museum of Natural History, but collected by Bartsch in 1930 fide Buden and Schwartz, 1968). Given the inconsistencies in how these two islands are labeled on maps (e.g., Google Earth 2011 imagery, accessed October 2017), it is plausible that all three individuals came from Elbow Cay. This population (or populations) was considered to represent *T. curtus* (originally *T. canus curtus* from the Bimini Islands and New Providence) after careful morphological analysis of the three known Cay Sal records and additional Bahamian material (Buden and Schwartz, 1968).

We find that mitochondrial and nuclear sequence data support the assertion that Elbow Cay *Tropidophis* are conspecific with *T. curtus* (Fig. 5). Because our sampling of the extensive geographic range of *T. curtus* is coarse grained, we are not able to estimate which populations on the Great Bahamas Bank are most closely related and thus potential progenitors of the Cay Sal population (e.g., Fig. 6), although morphological data suggest that the Bimini group or New Providence might be the likely origin (Buden and Schwartz, 1968). That the Cay Sal specimens differ morphologically from Androsian *Tropidophis* specimens (Buden and Schwartz, 1968; Hedges, 2002) is interesting if we expect that the Cay Sal population is the product of natural dispersal (see Fig. 1A for reference). However, it is a possibility, although not mentioned by previous authors (e.g., Buden and Schwartz, 1968), that the snakes were introduced to Elbow Cay during the construction of the lighthouse and associated buildings in the 19th century. Future studies on the phylogeography of this species could incorporate these sequence data to examine these hypotheses.

Of note, this species is considered mesophilic (Schwartz and Henderson, 1991; Hen-

derson and Powell, 2009), and is frequently found after periods of heavy rain or near semipermanent water sources, such as old wells (Henderson and Powell, 2009). Thus, its persistence on the xeric Cay Sal Bank is somewhat perplexing. Study of the natural history of this population is needed to determine how many individuals exist and whether they might differ behaviorally or physiologically from other Bahamian populations.

Additional squamate species. We were unable to locate two previously recorded species of terrestrial squamates from the Cay Sal Bank. The blindsnake *Typhlops biminien-sis biminien-sis* (Richmond, 1955; see Hedges et al., 2014; Pyron and Wallach, 2014 for taxonomic discussion) was collected on Elbow Cay (KUH 269649–269653) in 1967 by Thomas (1968b). The dwarf gecko *Sphaerodactylus nigropunctatus flavicauda* has been recorded from the Cay Sal Bank (Barbour, 1904; Buden and Schwartz, 1968; Thomas, 1968a; Thomas and Schwartz, 1974), although only from Elbow Cay (Buckner et al., 2012). Finally, a newly discovered population of *Cubophis cantherigerus* from the Anguilla Cays on the southeast edge of the Cay Sal Bank was reported in 2015 (Krysko et al., 2015). We did not visit the Anguilla Islands, although it is worth noting that this population derives from Cuban progenitors (on the basis of multilocus genetic analysis; Krysko et al., 2015).

Island accounts

Great Dog Rock. Great Dog Rock (24°1'48"N, 79°49'47.9994"W) is the largest of several islands marking the eastern edge of the Cay Sal Bank (Figs. 1, 2), and there were no previous herpetofaunal records from these islands (Buckner et al., 2012). These islands are largely devoid of vegetation and

low lying, and thus are likely washed over during hurricanes. Great Dog Rock is $< 1.0 \text{ km}^2$, with a patchy covering of ground vegetation. There is a single relatively large (5 m tall, 10 m wide) pyramid-shaped stand of *Cocoloba uvifera* near the center of the island (Fig. 7A). Sooty terns (*Onychoprion fuscatus*) and brown noddies (*Anous stolidus*) nest on the cay. We observed adult *A. sagrei* within the *Cocoloba* stand, and juveniles and small females on the ground near the scrub vegetation. We found a single juvenile underneath a discarded queen conch (*Strombus gigas*) shell. We did not observe any other terrestrial reptiles.

Cay Sal Island. Cay Sal ($23^{\circ}57'36''\text{N}$, $80^{\circ}26'23.9994''\text{W}$) is the largest island in the region ($\sim 1.7 \text{ km}$ long and $\sim 1.0 \text{ km}$ wide), and likely formed via the deposition of sediment on the southwestern side of the Cay Sal Bank owing to strong and consistent winds from the northeast, moving sand across the bank (Goldberg, 1983). There is a large salina and small brackish lake in the center of the island. Cay Sal previously housed a Bahamas immigration station, although it is now considered uninhabited. Nevertheless, the island is a major camping ground for illegal fishing boats (poachers). We saw ample signs of human disturbance—large trash accumulations, bottles, shotgun and handgun shell casings, and we observed a least one poaching vessel leaving the east side of the island after an overnight anchorage there. Cay Sal is heavily vegetated with silver palms (*Coccothrinax argentata*), mangroves, grasses, shrubs, and some coconut palms (Fig. 7B; also see Buden and Schwartz [1968] for an island description). The soil is sandy and a 10–17-m-high sand ridge runs northwest to southeast and is covered with patches of silver palms. We observed *A. fairchildi* between 0730h and 1200h in stands of silver palms lining a dense black (*Avicennia germinans*) and white (*Laguncularia race-*

mosa) mangrove stand. We found *A. sagrei* between 0930h and 1400h in most vegetation types. We observed abundant loggerhead sea turtle (*Caretta caretta*) tracks and turtle nesting activity on the beaches, and at least one nest appeared to have been excavated by a poacher (Fig. 8).

Elbow Cay. Elbow Cay ($23^{\circ}57'36''\text{N}$, $80^{\circ}26'23.9994''\text{W}$) is a relatively elevated island with the ruins of a 19th-century lighthouse and associated outbuildings. These outbuildings are now used to deposit people being trafficked toward the United States, as we observed during our visit. The island is rocky and is covered with low scrubby vegetation, except for a small *Casuarina* stand near the peak of the island (Fig. 7C). The island presently supports one of the largest known breeding colonies of Audubon's shearwaters (*Puffinus lherminieri*) and is a significant breeding location for at least three other seabird species (Mackin et al., 2015; Mackin, 2016). We found a very low abundance (fewer than 25 individuals) of *A. sagrei* near the *Casuarina* stand. Although there are records of *A. fairchildi* from Elbow Cay, we did not observe any individuals, and neither did Thomas in 1967 (Buden and Schwartz, 1968). This apparent absence of *A. fairchildi* is potentially owing to mislabeling of islands on the Cay Sal Bank. For example, Google Earth (2011 imagery, accessed October 2017) mislabels the Double Headed Shot Cays as Elbow Cay, whereas other references (e.g., Purkis et al., 2014; Krysko et al., 2015) do not explicitly label the cay itself. We observed a single *Tropidophis curtus* climbing from beneath a rock into a small shrub at 1025h. We did not observe *Typhlops* or *Sphaerodactylus*, both of which have been recorded from the island (Buckner et al., 2012).

East Double Headed Shot Cay. East Double Headed Shot Cay ($23^{\circ}59'23.9994''\text{N}$, $80^{\circ}20'24''\text{W}$), located 9

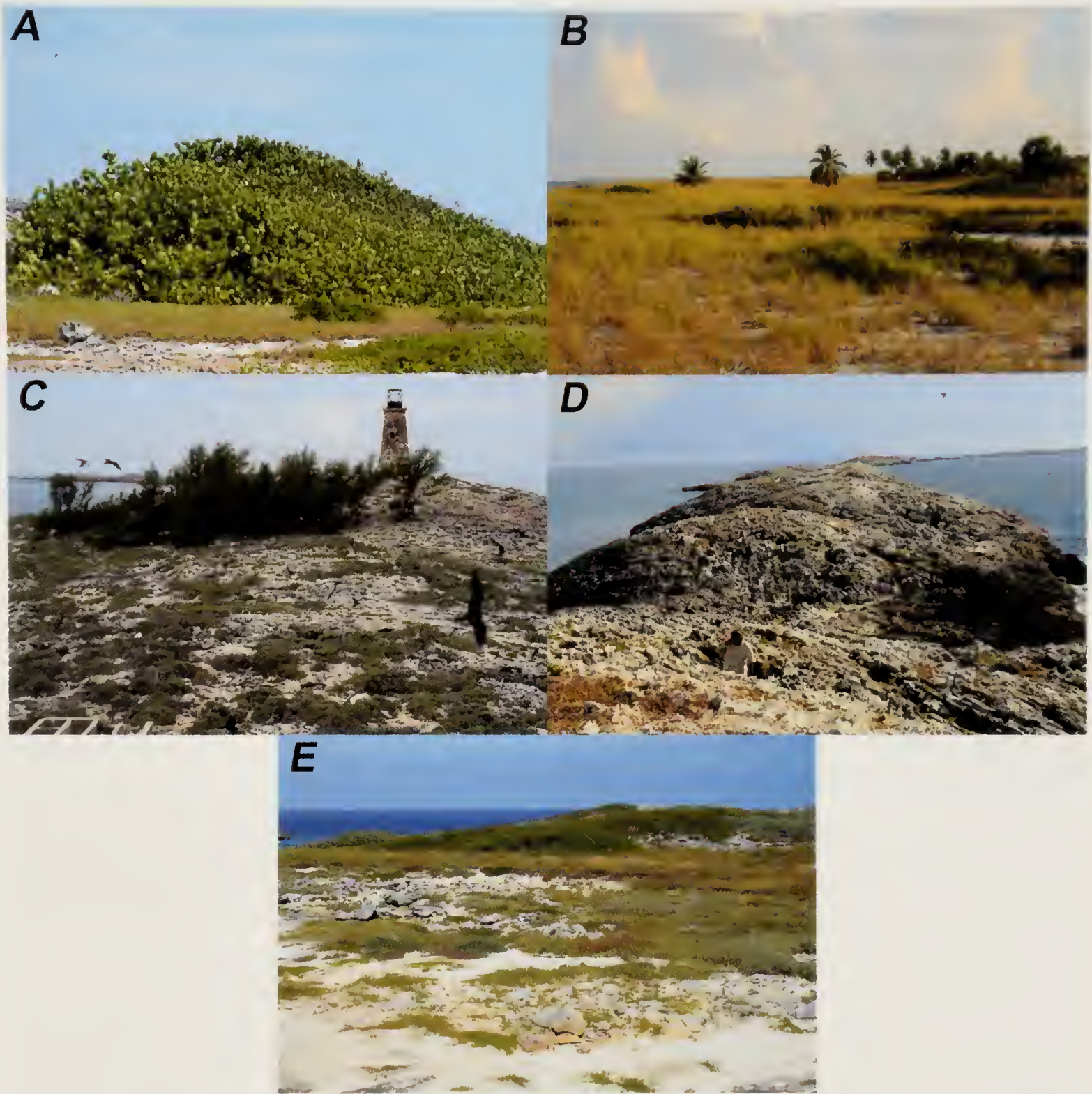


Figure 7. Islands surveyed on the Cay Sal Bank. A, *Cocoloba* stand on Great Dog Rock, the only significant vegetation on this tiny island. B, the southwestern side of Cay Sal Island, with the beach on the left and the ridge lined with palms and mangroves dropping to the salina on the right. C, the *Casuarina* stand on Elbow Cay, with nesting seabirds in the foreground. The lighthouse ruins on this island are frequently used to house people being trafficked across the Straits of Florida. D, Elephant Rocks, looking east toward Elbow Cay in the background. Note the steep slopes and relative lack of vegetation; this island is home to a saxicolous population of *Anolis sagrei*. ARPR is in the foreground for scale. E, Double Headed Shot Cay, with a view of the thick vegetation, rock piles, and sandy substrate. Photos by RGR and ARPR.

km northeast of Elbow Cay, is a component of the necklace of narrow islands forming the northern border of the Cay Sal Bank. This island (actually two islands separated by a

very small channel) is long and narrow (~2.8 km long and 15–25 m wide), with significantly more vegetation than other islands on the northern end of the bank. Parts of the



Figure 8. Loggerhead sea turtle (*Caretta caretta*) tracks on the southwest beach of Cay Sal Island. Note that the nest has been excavated by a poacher.

island are quite lush with low vegetation thick enough that it is difficult to penetrate (Fig. 7D). Some larger mangroves (*L. racemosa*) are also present. A single herpetofaunal record exists for this island: *Tropidophis*

curtus. We did not observe this species, although we found a generally low abundance of *A. sagrei*, and did not observe any other species of reptiles.

Elephant Rocks. Elephant Rocks (23°55'47.9994"N, 80°28'11.9994"W) are a series of cays west of Elbow Cay defining the northwestern edge of the Cay Sal Bank (Fig. 2). The islands are relatively tall and very narrow and provide habitat for large densities of brown boobies (*Sula leucogaster*), sooty terns, and brown noddies. Vegetation is scant and what scrub does exist is very low to the ground or grows in crevices. The terrain is steep and requires scrambling up and down jagged cliffs (Fig. 7E). No herpetofaunal records exist for these islands as far as we are aware (Buckner et al., 2012), an unsurprising situation given the apparent lack of suitable habitat and hazardous landing conditions. Nevertheless, we discovered *A. sagrei* on two of these cays, although in low abundance. All the individuals we observed were using rocks and small caves as cover and refuge, and were very shy when approached. This is apparently a saxicolous population of *A. sagrei* and warrants further study.

Conclusions

A great deal is known about the impact of dispersal on intra- and interspecific diversi-

TABLE 2. TAXONOMY OF CAY SAL BANK TERRESTRIAL HERPETOFAUNA AND LIKELY BIOGEOGRAPHIC ORIGINS OF EACH LINEAGE.

Species	Origins	New Taxon	Old Taxon
<i>Anolis sagrei</i>	Western Cuba	<i>Anolis sagrei sagrei</i>	<i>Anolis sagrei ordinatus</i>
<i>Anolis fairchildi</i>	Western Cuba	—	<i>Anolis fairchildi</i>
<i>Tropidophis curtus</i>	Great Bahamas Bank	—	<i>Tropidophis curtus</i>
<i>Cubophis cantherigerus</i>	Cuba	—	<i>Cubophis cantherigerus</i>
<i>Sphaerodactylus nigropunctatus</i>	Great Bahamas Bank (presumed)	—	<i>Sphaerodactylus nigropunctatus flavicauda</i>
<i>Typhlops biminienensis</i>	Great Bahamas Bank (presumed)	—	<i>Typhlops biminienensis biminienensis</i>

fication in West Indian *Anolis* lizards (Losos, 2009), yet many species and populations remain understudied. On the remote Cay Sal Bank, we find that the two species of anoles occurring there are a product of dispersal from western Cuba, contrary to the previously assumed Bahamian origin for *A. sagrei*. Although we refrain from sinking the specific epithet *A. fairchildi* into *A. porcatus*, largely owing to the necessity for further systematic study of the *porcatus* complex (Glor et al., 2005), we do recognize the brown anole populations as *A. sagrei* instead of *A. sagrei ordinatus* (Table 2). We further find that the *Tropidophis* snake from Elbow Cay is likely conspecific with Great Bahamas Bank *T. curtus*. Finally, we have added new island herpetofaunal records for the region, although we note that invasive predators (*Rattus* sp.) are recorded from most islands in the region and could be affecting terrestrial and marine reptiles (Mackin et al., 2015).

CONFLICT OF INTEREST

The authors declare that they have no conflict of interest.

ACKNOWLEDGMENTS

We thank Captain Wasson and the crew of the M/V *Spree* for transit to and from the Cay Sal Bank, zodiac runabout services, and safety oversight. We especially thank Jonathan Losos for advice and support for travel to the region, as well as the support of the Museum of Comparative Zoology. We are grateful for funding from the Putnam Fund for Research and Exploration from the Museum of Comparative Zoology (to RGR), as well as the John Templeton Foundation (to Jonathan B. Losos). We thank the Bahamas Department of Agriculture, the Bahamas Environment, Science and Technology Commission, Ministry of the

Environment, and the Bahamas National Trust for research and export permits. We also thank Sandra Buckner for discussions and advice related to this work.

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